

SEXUAL AND AGONISTIC BEHAVIOR OF THE COMMON RHEA

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THE behavior of a group of Common Rheas (*Rhea americana*) was studied during 1962 and 1963 in large outdoor enclosures at the Detroit Zoological Park and the San Diego Zoo. The maintenance behavior of this species was described in an earlier paper (Raikow, 1968) and the present paper deals with aggressive behavior, courtship, and nesting.

AGONISTIC BEHAVIOR

Individual Distance.—Except during agonistic or reproductive activities when contact is necessary, each rhea maintains a zone of a few inches around itself into which other rheas are not permitted to come. This individual distance is maintained by one rhea moving slightly away from another when they are standing or moving about in a group. During periods of excitement, as when rheas are gathered together to be fed by zoo visitors, casual and momentary bodily contact may occur without any reaction. However, if one bird pushes against another it may elicit a Head-forward threat display.

Head-forward Display.—When a rhea sits down the individual distance may increase to enclose the animal in a circle with a radius of several feet. The size of this circle varies with factors which are not clearly understood, but seem to involve sex, reproductive state, and the kind of intruder. Males are more apt to be aroused than are females. At times a resting rhea is completely unresponsive to the approach of another, but often it reacts with a Head-forward threat display. As the intruder approaches to within 20 feet or so the resting bird becomes alert and carefully watches the other. If the intruder comes no closer the rhea relaxes and resumes its rest. However if the other approaches to within 10 or 15 feet the rhea opens its bill and gapes, drawing its head back slightly and turning it so as to face the moving rhea continually. Again, if the intruder comes no closer, the rhea resumes its rest. More commonly, however, the resting bird will thrust its head toward the intruder with bill agape, often hissing loudly, then quickly draw its neck back into an S-curve. This may be repeated several times. (Fig. 1)

The response of other animals to this display is extremely mild. A rhea or llama which is wandering past only occasionally glances at the displaying bird, and usually ignores it completely.

If the intruder remains nearby for more than a minute or two the rhea may rise to the crouching position or even stand up. Having gotten to its feet it seems to lose its belligerency and may preen for a moment before wandering off with no further interest in the other individual.

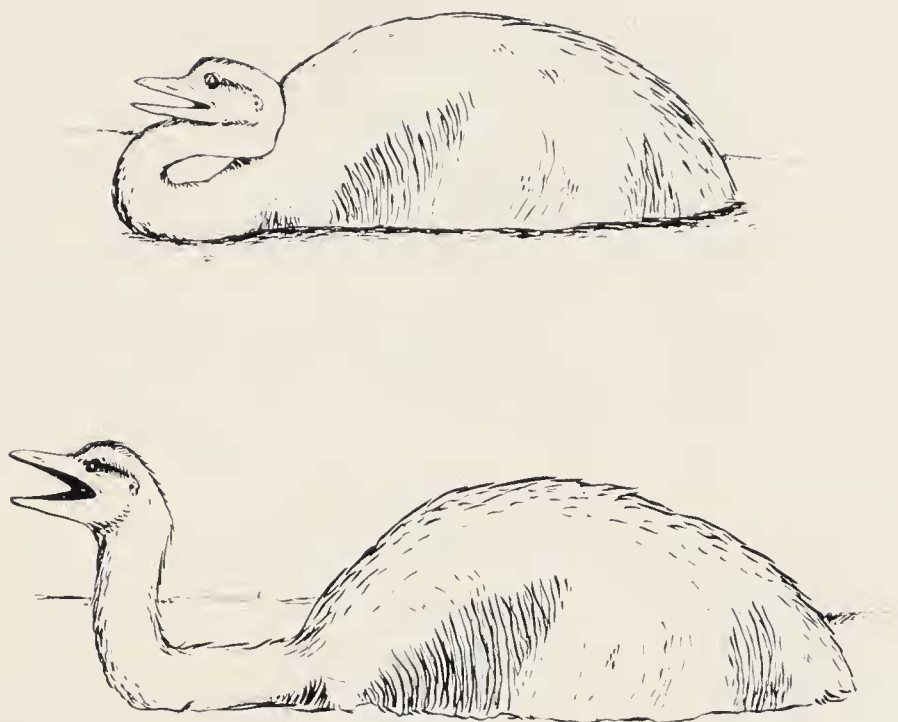


FIG. 1. The Head-forward Threat Display of the male rhea.

Discussion.—The Head-forward movement appears to be a ritualized act of biting, and includes various more-or-less modified components of the act. These are as follows:

- a. Gaping and thrusting the head forward are intention movements of biting.
- b. Hissing is presumably useful in intimidation, but its origin is not clear. Possibly it is derived from normal breathing activity, i.e., an exaggerated expiration sound (See Spurway and Haldane, 1953).
- c. Beak-snapping occurs during threat displays in some birds, e.g., the Chaffinch (Marler, 1956), and is an intention movement of biting. It occasionally occurs in the rhea at the end of the forward neck thrust.
- d. Wing-spreading occasionally occurs during the Head-forward display of a rhea on the ground. It may have some intimidation value by increasing the rhea's apparent size, or because of the sudden movement. This movement is common in nest defense where the spread wings cover the eggs or chicks, and sometimes occurs in a display by a male which is lying down but is not on a nest. Perhaps this inappropriate movement occurs because of the postural similarity of the two situations.

The various components of the display occur at different levels of motivation, resulting in a regular sequence of movements. The level of motivation increases as the external stimulation continues, and under low motivation the display is performed more slowly and may not be completed. Gaping

is the first of the components to occur, and is thus the movement which is initiated at the lowest level of motivation. Under low motivation the subsequent movements of withdrawal and thrusting the head forward occur slowly, but under higher motivation the pauses between components disappear, and the entire act is performed in one quick, coordinated movement.

The cause of this reaction is uncertain. A rhea which is on the ground is more vulnerable to attack than when on its feet, so an increased alertness is probably of adaptive value. The greater sensitivity of males is possibly related to a state of broodiness, for a male on the ground during the breeding season may be sensitive to situations which might endanger the nest, if it had one.

REPRODUCTIVE BEHAVIOR

The most conspicuous aspect of the reproductive behavior of the rhea is the dominant part played by the male. He performs courtship displays, builds the nest, incubates the eggs, and cares for the chicks. The female's role is limited to copulation and egg-laying. The rhea is both polygynous and polyandrous and apparently no pair-bonds are formed beyond the momentary association of copulation. Females lay eggs in the nests of various males, and if no male is ready with a nest the egg is simply dropped somewhere. The young are precocious and able to feed themselves almost from hatching, but must be protected by the male against predation.

Sexual Rivalry Between Males.—The breeding season is marked by an intense sexual rivalry between males. Hudson (1920) has noted that in the wild the younger males may be "attacked and driven off" by older males, and has described the combat which occurs between older males, in which they twist their necks together and bite viciously while running together in a circle. Such fighting was not observed in this study, possibly because one male established dominance over the others. There were four full-grown males in the group, but only two attempted to establish nests, and only one was seen attempting copulation or guarding eggs.

Chasing of other males was common. First the male stands in a characteristic threat posture with the front of the body lowered, the neck held in a low U-loop, and the eyes fixed on the other rhea. (Fig. 2) Then he extends his head forward and takes a few slow steps toward the other before breaking into a run. Often a less intense display is seen, in which the lowering of the body consists of a single, rapid bobbing motion, and the Head-forward Display merges quickly into a run without the initial walking steps.

As the pursuer runs he holds his wings raised above his back and his neck in an S-curve, thrusting it forward to bite when he gets close enough. Often he aims at the other's head, hitting it or missing by a few inches. The pursued rhea runs off in a characteristic defense posture with his neck drawn back

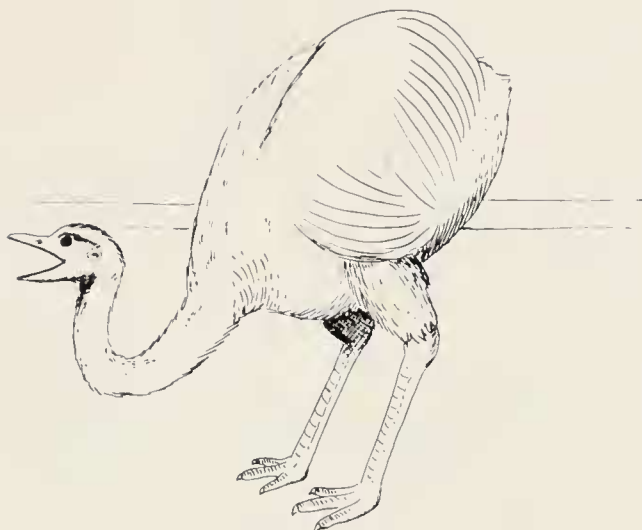


FIG. 2. The threat posture of the male rhea.

in an S-curve and his wings held high above his back, or sometimes spread laterally, and often flicked up and down rapidly and sporadically. He makes frequent sharp changes in direction, resulting in a zig-zag path of escape. This differs somewhat from the defense posture described by Portielje (1925) in which the wings are not fluttered and the neck is held upright rather than drawn back. This occurs when the rhea is not too excited. Wing flipping begins when the attacker draws near, and perhaps helps the pursued male to avoid being bitten. A chase seldom exceeds thirty or forty feet in length.

Courtship Display.—The Call Display involves three consecutive activities: (a) assumption of a call posture, (b) the call itself, and (c) a running display. The first indication of rising sexual drive in the male is a ruffling of the plumage of the head and upper neck. This may occur at almost any time, e.g., during feeding. It may be followed by later stages of the display, or may gradually disappear. The male may show the same ruffling prior to the wing display, described below, or before chasing another male.

As the level of motivation rises the ruffling of plumage extends to other areas, including the base and middle of the neck, the breast, the tibiae, the back, and the rump. The wings are then extended dorso-laterally. The rhea may remain at this stage for several seconds and then relax his plumage, or the next stage of the display may follow.

The actual display begins with a characteristic posture. (Fig. 3) The anterior end of the body is raised upward. The neck is held stiffly upward and forward, with the plumage ruffled to a maximum degree. The wings may be raised higher than before, and the base of the neck is expanded. The call is then given, sometimes immediately and sometimes after a pause of several seconds. The call is deep-toned, with two notes, and lasts about



FIG. 3. The Call Display of the male rhea.

one second. The first note is the deeper of the two, and falls in pitch, while the second note rises slightly higher than the first. It has been described as a deep-toned hissing (Darwin, 1955), the last tone of a siren (Portielje, 1925), and a deep booming (Wetmore, 1926). After calling once or twice the rhea may relax, or it may break into a run of several hundred feet, sometimes flipping the wings up and down alternately. One wing may be held higher than the other, and the rhea may change directions suddenly. This running is similar in appearance to the defense run described above. The male runs toward the female from behind or to one side, at which the female runs off with the male following. Portielje (1925) described the female as running *toward* the male, but this was not observed here. Her bearing is so like the defense posture that the performance has more the appearance of an aggressive chase than a courtship ritual, and perhaps the female so regards it when her reproductive drive is low.

Sometimes a male performs an incomplete, or even a complete call display when no female is nearby. Possibly this is a vacuum activity, but since there are always females around, though perhaps no nearer than several hundred feet, it may be that the male is responding to a visual stimulus. In any event it is clear that this display may be performed with only a very minimal ex-



FIG. 4. (a and b). The Wing Display of the rhea. The bird with its wings spread laterally is the male, the other a female.

ternal stimulus. In contrast, the other courtship displays occur only when another rhea is nearby.

Presumably the function of the call is to attract the attention of the female. It is apparently the only vocalization in this species other than the peeping of the chicks, hissing during threat, and some grunts used by the male to warn the chicks of danger. Why does it occur in this generally silent animal? Perhaps because these birds, living in groups in open country are in full view of each other much of the time, and are so accustomed to seeing other rheas that some unusual and highly specific signal is needed to overcome this familiarity so that the female's attention will be actively drawn to the display.

The male makes no attempt to copulate after running, but generally shows no further interest in the female. Possibly the major function of the display is the long-term stimulation of the female's reproductive drive.

In the Wing Display the male slowly approaches the female, lowers his neck in a low loop, and walks beside her, sometimes bobbing his head slightly. The plumage of his head and upper neck is ruffled. This may continue for several minutes while both birds peck and nibble at objects on the ground. Finally the male spreads his wings and walks beside or ahead of the female in the full display (Fig. 4) with the anterior end of the body lowered slightly and the neck in a low U-curve. The wings are extended laterally and slightly forward, at about right angles to the longitudinal axis of the body. The humerus extends out from the body and droops slightly, the radio-ulna is directed vertically downward, and the manus is extended outward and down at about a forty-five degree angle. Often the wings are held so low that the plumes drag on the ground. The plumage of the head and

neck is generally heavily ruffled, while that of the back, flanks, rump, and tibiae are sometimes more lightly ruffled.

The male walks slowly beside the female, sometimes turning to give her a front view of his wings. The female may be unresponsive, though if the male persists she may walk quickly away. The display usually lasts ten to fifteen seconds, but sometimes persists for as long as two minutes. Longer displays reflect stronger motivation, for the posture is more stiffly maintained, the ruffling of feathers is at a maximum, and the male may perform a few head-bobbing movements as he walks. Most displays end when the female walks away, at which the male often engages in wing-preening. Occasionally the male may attempt to begin copulation, but the female generally evades him. He does so by grasping her at the base of the neck with his bill. Almost always she pulls away and runs off. As a result it is common to see females during this time with the base of their neck plucked free of feathers.

This display probably arose through the ritualization of displacement activities arising from approach-avoidance conflict. The most conspicuous component of the display is wing-spreading. The only non-display activity of this species which results in a similar wing posture is wing-preening. It would appear that the Wing Display is a ritualized wing-preening movement in which wing-spreading has been emphasized while the preening movements with the bill have been inhibited. These may occur, however, if the female responds negatively and the male is unable to attempt copulation. Early in the course of evolution of this display other displacement activities could have occurred during approach-avoidance conflict. The Wing Display, however, was presumably selected for because it was most effective as a social signal, probably because it is more distinct and unique than other movements, i.e., it results in the greatest change in the appearance of the male.

This kind of sexual display may have lead to the retention of the wings in this species during the course of evolution, despite the fact that they no longer served in locomotion. In such ratites as the emu, in which the wings are reduced to small vestiges, no such selection pressure apparently existed.

Regarding the other components of the Wing Display, the ruffling of the plumage is probably a ritualized expression of the autonomic pilomotor response to excitement (Morris, 1956), while Head-bobbing may represent either intention movements of the inhibited preening activity, or an intention movement of grasping the female. The pecking at the ground which sometimes occurs early in the display is presumably a displacement feeding activity.

The Head-bobbing Display of the male is apparently performed under sexual motivation, since it is usually directed toward a female. The male stands with the neck in a low loop. The head and neck are bobbed vigorously

up and down through a path of about a foot in the sagittal plane, and sometimes simultaneously swung from side to side through a U-shaped arc in the transverse plane. This Head-bobbing is like that sometimes seen in the Wing Display, but greatly exaggerated.

The display is directed only toward a rhea which is sitting down, usually a female. She immediately becomes alert, rises to her heels, and a moment later to her feet. She may preen a bit after arising, and sometimes also bobs her head slightly. After arising she usually walks away. Often the male follows and performs a Wing Display, or intention movements of one. Once a male grasped a female at the base of the neck in an attempt to initiate copulation, but the female pulled free. Sometimes instead of arising slowly the female will leap suddenly to her feet and run away rapidly in the defense posture.

The most likely explanation for this behavior seems to be that it is a precopulatory display stimulated by the sight of a female on the ground, the position which she maintains during copulation. The Head-bobbing may be a ritualized intention movement of grasping, which initiates copulation.

Copulation.—Successful copulation was not observed during this study. Portielje (1925) gives the following description (translated):

"During the quite extended copulation the hen lay on the ground with her neck stretched forward. The cock did not mount her, but sat behind her, propped up on his heels while holding the feathers of her lower neck with his beak, and from time to time making violently thrusting motions."

Brito (1949) notes that the act averages two minutes in duration.

Nest Construction.—The nest is roughly circular, about three feet across, and about one foot deep. In nature it is often placed in some shaded area or in tall grass (Wetmore, 1926). In the zoo, nests were constructed in both sunny and shaded areas, but eggs were laid only in the latter.

In constructing his nest, the male digs by kicking backward with his feet, either while standing or crouching in the nest. Movements of the body while crouched undoubtedly aid in shaping the nest. A low rim of loose material is raised slightly above the surrounding soil, and is often arranged with twigs or leaves. Some dirt may also be removed with the bill.

Nest Ceremony and Egg-Laying.—According to Sick (1964) and Steinbacher (1951) the male leads the female to the nest for egg-laying. This was also observed once during the present study, but in several other instances the female approached the male as he sat on the nest. The male responds to this approach by watching her closely, often rising to his heels. She approaches the edge of the nest and slowly walks around it, sometimes pausing to stand perfectly still for several minutes at a time. The male may rise to his feet, but usually remains sitting or crouching, twisting his neck grotesquely

in his attempts to keep the female in view. He may even extend his neck straight out over his back, peering directly behind himself with his head upside-down. Usually during the first several minutes of this confrontation the male makes threat movements, crouching low and spreading his wings to cover the nest while giving Head-forward displays and snapping at the female. She does not return the attack but remains outwardly calm, often immobile. After several minutes the character of the male's activity changes. The aggressive movements are replaced by a more ritualized display with vigorous Head-bobbing and neck swinging movements. The female may respond with a very faint Head-bobbing, and the male still twists his neck around to follow her movement around the nest.

Finally the female crouches on her heels beside the male and deposits the egg on the rim of the nest. Her cloaca is held a few inches above the ground and the egg is deposited gently. Portielje (1925) describes an act in which the male extends one wing beneath the female's cloaca, catching the egg as it is dropped so as to cushion its fall. Such behavior was not observed in this study. Immediately after laying the egg the female rises and walks or runs away. The male then draws the egg beneath himself with his bill. As the male broods he alternately sleeps and is alert, holding his head high and looking about. Sometimes he sleeps deeply for half an hour or more with his neck folded in an S-curve, but mostly he holds his neck vertically and naps only for a few seconds, or one or two minutes at most.

In both sexes agonistic as well as reproductive motivation is present, and the aggressive drives must be reduced before reproductive behavior can occur. At first the male is agonistically motivated, and shows conflicting tendencies to attack (shown by the Head-forward Display) and to remain on the nest (shown by the crouching and wing-spreading). This is because the female presents both aggressive and reproductive stimuli. In order to reduce the male's aggressive reactions she must provide additional reproductive stimulation, in the form of some type of submissive behavior (Tinbergen, 1952). She does this by failing to respond to the male's threat display with a normal defense reaction. Instead she becomes almost immobile, and stands quietly or moves only slowly for several minutes, until the male begins to relax. As his aggressiveness wanes, the Head-forward threat movements are replaced by Head-bobbing and neck swinging which are probably ritualized Head-forward Displays. This apparently acts as a releaser, permitting the female to cease her submissive behavior and to continue on to the act of egg-laying. Once she has laid the egg, the female is no longer reproductively motivated, and she leaves.

Sometimes a female will approach a male on the nest, the ritual will occur, and then she will walk away without having crouched or laid an egg. Here



FIG. 5. The nest-defense posture of the male rhea.

her reproductive drive may be insufficient to overcome her reaction to the male's aggressiveness so that crouching beside him, which involves the suppression of her normal tendency to maintain an individual distance, cannot take place.

Nest Defense.—A characteristic threat display is given by an incubating male if he is aroused by the approach of another rhea. Crouching low on the nest, he spreads his wings laterally, holding them closely appressed to the ground, and covering the eggs, while at the same time giving a Head-forward threat display (Fig. 5). This is very similar to the purely aggressive threat display described above, with the addition of the nest-covering wing movement. It is also similar to the early part of the male's reaction to a female who approaches for the purpose of egg-laying, and undoubtedly that response is a little-modified Nest-defense Display. However in true nest defense the male is much fiercer in appearance, his posture is more stiffly maintained, and his movements are jerkier, indicating a greater intensity of aggressiveness.

SUMMARY

A group of Common Rheas was studied in a large outdoor enclosure at the Detroit zoo. A small individual distance is maintained, but the major defensive display is a head-forward movement derived by ritualization of biting movements. In Nest-defense this includes a nest-covering movement of the wings.

The male performs three types of displays. A Call Display begins with a booming call given in an upraised posture with the wings raised and the base of the neck swollen. The rhea then runs across the enclosure in a zig-zag course. He may chase a female, who then runs away in a similar manner, or may perform the display alone. It seems likely that the running phase is derived from an aggressive chase, and probably the female regards it as such. The function of this display is uncertain, perhaps it acts in long-term stimulation of the female.

The Wing Display is always directed toward a female, and may lead to copulation. The male walks beside the female with his neck in a low U-loop and his wings spread laterally. Then he may grasp the female at the base of her neck in an attempt to begin copulation, but the female usually runs away. The origin of this display may be the wing-preening posture of the male, which arises as a displacement activity resulting from approach-avoidance conflict prior to copulation.

A Head-bobbing Display of the male is directed toward a seated female. It may be a precopulatory display, but its origin is uncertain.

When the female is ready to lay an egg she comes to the nest and the male at first reacts aggressively, but gradually his defensive movements assume the appearance of a formalized display, permitting the female to approach closely. She crouches beside the male and lays the egg, then walks away, taking no further part in reproduction.

The nest is a shallow hole in the ground three or four feet wide and sometimes lined with a bit of loose vegetation. The male spends some time in it, resting or "defending" it against other rheas, even though it may contain no eggs.

In some ratites the wings are reduced to functionless vestiges, but in the rhea they are utilized in sexual displays and have apparently been retained by selection because of their value as a secondary sexual characteristic, rather than in their original function as locomotory structures.

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